Updating the sulcal landscape of the human lateral parieto-occipital junction provides anatomical, functional, and cognitive insights

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Abstract

Understanding the tripartite relationship among neuroanatomy, brain function, and cognition is of major interest across neurobiological subdisciplines. Recent advances in neuroimaging have uncovered neuroanatomical structures in evolutionarily-expanded portions of the brain that are related to individual differences in brain function and cognition. Here, we explored this relationship in lateral parietal cortex (LPC), a region crucial for many higher-level cognitive abilities. To do so, we manually defined 2176 individual sulci across 144 hemispheres. We identified four small and shallow indentations of the cerebral cortex (sulci) that were previously unidentified in the lateral parieto-occipital junction (LPOJ) and LPC. One of these sulci (ventral supralateral occipital sulcus, slocs-v) is present in nearly every hemisphere, and is morphologically, architecturally, and functionally dissociable from neighboring sulci. Implementing a data-driven, model-based approach relating sulcal depth to behavior identified different relationships of ventral and dorsal LPC/LPOJ sulcal networks contributing to the perception of spatial orientation. The model identified the slocs-v, further indicating the importance of this new neuroanatomical structure. Our findings build on classic neuroanatomical theories and identify new neuroanatomical targets for future “precision imaging” studies exploring the relationship among brain structure, brain function, and cognitive abilities at the level of the individual participant.

Keywords

Cortical folding, Functional neuroanatomy, Magnetic resonance imaging (MRI), Occipital cortex, Parietal cortex, Spatial orientation

Introduction

A fundamental goal in neuroscience is to understand the complex relationship between brain structure and brain function, as well as how that relationship provides a scaffold for efficient cognition and behavior. Of all the neuroanatomical features to target, recent work shows that morphological features of hominoid-specific, shallow indentations, or sulci, of the cerebral cortex are not only functionally and cognitively meaningful, but also are particularly impacted by multiple brain-related disorders and aging [1–20]. The combination of these findings provides growing support for a classic theory proposing that the late emergence of these structures in gestation within association cortices, as well as their prolonged development, may co-occur with specific functional and microstructural features that could support specific cognitive abilities that also have a protracted development [21]. Nevertheless, despite the developmental, evolutionary, functional, cognitive, and theoretical relevance of these findings, they have mainly been restricted to only a subset of association cortices such as the prefrontal, cingulate, and ventral occipitotemporal cortices [1–20]. Thus, examining the relationship among these structures (also known as tertiary sulci) relative to architectonic and functional features of the cerebral cortex, as well as relative to cognition, remains uncharted in other association cortices such as the lateral parietal cortex (LPC).

As LPC is a cortical extent that has expanded extensively throughout evolution [22,23], there is great interest in the structure and function of LPC in development, aging, across species, and in different patient populations. Yet, key gaps in knowledge relating individual differences in the structure of LPC to individual differences in the functional organization of LPC and cognitive performance remain for at least four main reasons. First, one line of recent work shows that LPC displays a much more complex sulcal patterning than previously thought [24–27], while a second line of work shows that LPC is tiled with many maps and discrete functional

regions spanning modalities and functions such as vision, memory, attention, action, haptics, and multisensory integration in addition to theory of mind, cognitive control, and subdivisions of the default mode network [28–34]. Second, a majority of the time, the two lines of work are conducted independently from one another and the majority of human neuroimaging studies of LPC implement group analyses on average brain templates—which causes LPC sulci to disappear (**figure 1**). Third, despite the recently identified complexity of LPC sulcal patterning, recent studies have also uncovered previously overlooked tertiary sulci in association cortices (for example, in the posterior cingulate cortex [13,15]). Thus, fourth, it is unknown if additional LPC tertiary sulci are waiting to be discovered and if so, could improve our understanding of the structural-functional organization of LPC with potential cognitive insights as in other association cortices. Critically, while such findings would have developmental, evolutionary, functional, cognitive, and theoretical implications for addressing novel questions in future studies, they would also have translational applications as sulci serve as biomarkers in neurodevelopmental disorders [3–6] and “corridors” for neurosurgery [35,36].

In the present study, we first manually defined LPC sulci in 144 young adult hemispheres using the most recent definitions of LPC sulci [24]. By manually labeling over 2,000 sulci, we uncovered four previously undefined (Supplemental Methods and Supplemental figures 1-4 for historical details) sulci in the cortical expanse between the caudal branches of the superior temporal sulcus (cSTS) and two parts of the intraparietal sulcus (IPS)—a cortical expanse recently referenced as containing sensory “bridge” regions of the temporal-parietal-occipital junction [37]—which we term the supralateral occipital sulci (ventral: slocs-v; dorsal: slocs-d) and posterior angular sulci (ventral: pAngs-d; dorsal: pAngs-d). We then utilized morphological (depth and surface area), architectural (gray matter thickness and myelination), and functional (resting-state functional connectivity) data available in each participant to assess whether the most common of these structures (slocs-v) was dissociable from surrounding sulci.

Finally, we assessed whether the updated view of the LPC/LPOJ sulcal landscape provided cognitive insights using a model-based, data-driven approach [17] relating sulcal morphology to behavior on tasks known to activate regions within this cortical expanse (for example, reasoning and spatial orientation [38–41]).

Materials and Methods

(a) Participants

Data for the young adult human cohort analyzed in the present study were from the Human Connectome Project (HCP) database (https://www.humanconnectome.org/study/hcp-young-adult/overview). Here, we used 72 participants (50% female, 22-36 years old, and 90% right-handed; there was no effect of handedness on our behavioral tasks; Supplemental materials) that were also analyzed in several prior studies [11–16].

(b) Neuroimaging data acquisition

Anatomical T1-weighted (T1-w) MRI scans (0.8 mm voxel resolution) were obtained in native space from the HCP database. Reconstructions of the cortical surfaces of each participant were generated using FreeSurfer (v6.0.0), a software package used for processing and analyzing human brain MRI images (surfer.nmr.mgh.harvard.edu) [42,43]. All subsequent sulcal labeling and extraction of anatomical metrics were calculated from these reconstructions generated through the HCP's version of the FreeSurfer pipeline [44].

(c) Behavioral data:

In addition to structural and functional neuroimaging data, the HCP also includes a wide range of behavioral metrics from the NIH toolbox [45]. To relate LPC/LPOJ sulcal morphology to behavior, we leveraged behavioral data related to spatial orientation (Variable Short Penn Line

Orientation Test), relational reasoning (Penn Progressive Matrices Test), and processing speed (Pattern Completion Processing Speed Test; Supplemental Methods for task details). We selected these tasks as previous functional neuroimaging studies have shown the crucial role of LPC/LPOJ in relational reasoning and spatial orientation [38–41], while our previous work relating sulcal morphology to cognition uses processing speed performance as a control behavioral task [17,19].

(d) <u>Anatomical analyses:</u>

(i) *Manual labeling of LPC sulci*

Sulci were manually defined in 72 participants (144 hemispheres) guided by the most recent atlas by Petrides [24], as well as recent empirical studies [25–27], which together offer a comprehensive definition of cerebral sulcal patterns, including tertiary sulci. For a historical analysis of sulci in this cortical expanse, please refer to Segal & Petrides [25] and Zlatkina & Petrides [26]. Our cortical expanse of interest was bounded by the following sulci and gyri: (i) the postcentral sulcus (PoCS) served as the anterior boundary, (ii) the superior temporal sulcus (STS) served as the inferior boundary, (iii) the superior parietal lobule (SPL) served as the superior boundary, and (iv) the medial and lateral transverse occipital sulci (mTOS and lTOS) served as the posterior boundary. We also considered the following sulci within this cortical expanse: the three different branches of the caudal superior temporal sulcus (posterior to anterior: cSTS3, 2, 1), the supramarginal sulcus (SmgS), posterior intermediate parietal sulcus (pips), sulcus of Brissaud (sB), anterior intermediate parietal sulcus of Jensen (aipsJ), paroccipital intraparietal sulcus (IPS-PO), intraparietal sulcus (IPS), and the superior parietal sulcus (SPS). Of note, the IPS-PO is the portion of the IPS extending ventrally into the occipital lobe. The IPS-PO was first identified as the paroccipital sulcus by Wilder (1886). There is often an annectant gyrus separating the horizontal portion of the IPS proper from the IPS-PO [26,46].

Additionally, we identified as many as four previously uncharted and variable tertiary LPC/LPOJ sulci for the first time: the supralateral occipital sulcus (slocs; composed of ventral (slocs-v) and dorsal (slocs-d) components) and the posterior angular sulcus (pAngs; composed of ventral (pAngs-v) and dorsal (pAngs-d) components). In the Supplemental Methods and Supplemental Figures 1-4, we discuss the slocs and pAngs within the context of modern and historical sources.

For each participant in each hemisphere, the location of each sulcus was confirmed by trained independent raters (E.H.W., Y.T., and T.G.) and finalized by a neuroanatomist (K.S.W.). All LPC sulci were then manually defined in FreeSurfer using tksurfer tools, as in previous work [11–20], from which morphological and anatomical features were extracted. For four example hemispheres with these 13-17 sulci identified, see **figure 1*a*** (Supplemental figure 5 for all hemispheres). The specific criteria to identify the slocs and pAngs are outlined in **figure 1*b***. We also generated sulcal probability maps for each sulcus (Supplemental Methods and Supplemental figure 6).

To test whether the incidence rates of the slocs and pAngs components were statistically different, we implemented a binomial logistic regression GLM with sulcus (slocs-v, slocs-d, pAngs-v, and pAngs-d) and hemisphere (left and right), as well as their interaction, as predictors for sulcal presence [0 (absent), 1 (present)]. GLMs were carried out with the glm function from the built-in stats R package. ANOVA $\chi 2$ tests were applied to each GLM with the Anova function from the car R package, from which results were reported.

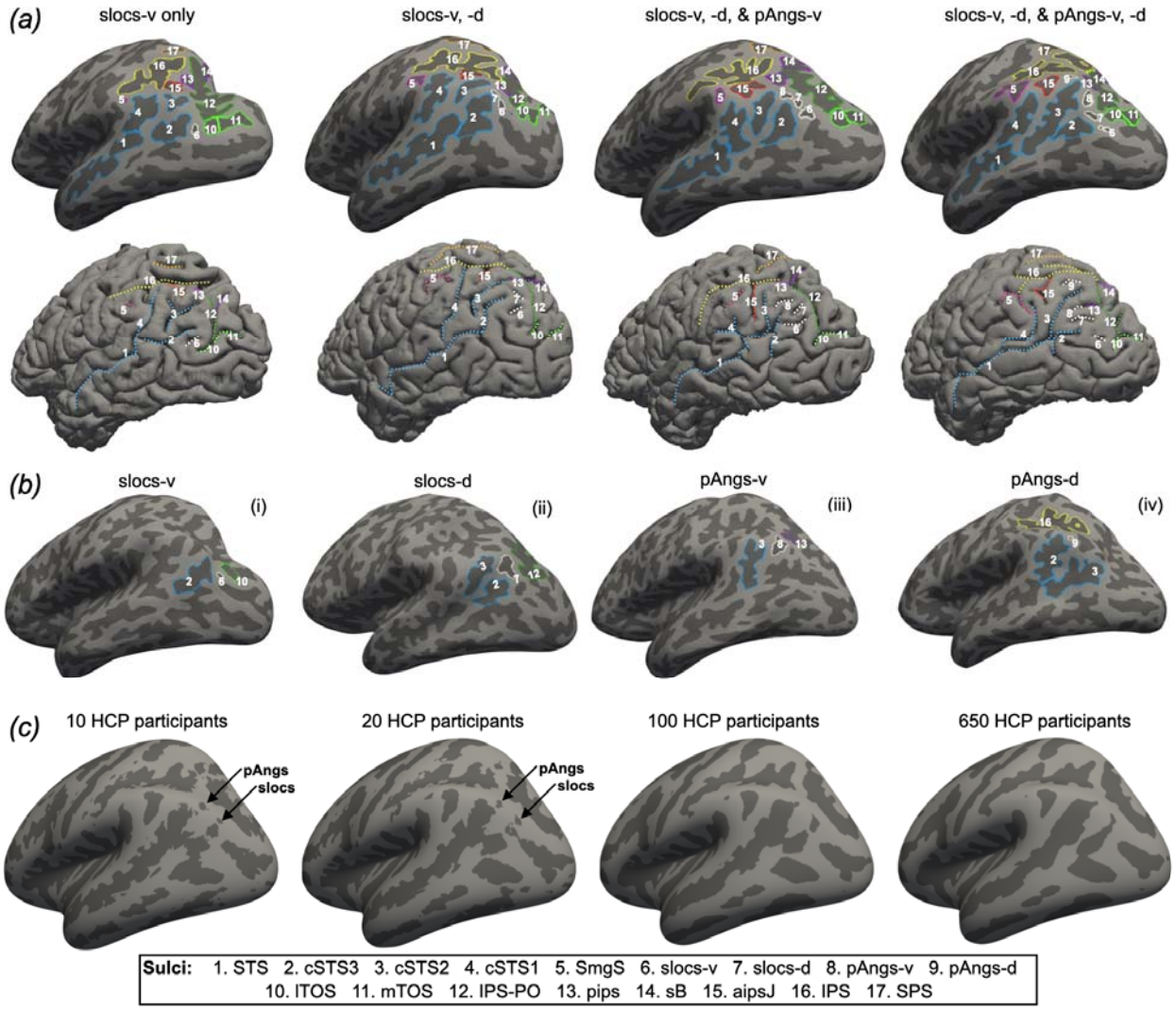

Figure 1. Four previously undefined small and shallow sulci in the lateral parieto-occipital junction (LPOJ). *(a)* Four example inflated (top) and pial (bottom) left hemisphere cortical surfaces displaying the 13-17 sulci manually identified in the present study. Each hemisphere contains 1-4 of the previously undefined and variable LOC/LPOJ sulci (slocs and pAngs). Each sulcus is numbered according to the legend. *(b)* Criteria for defining slocs and pAngs components. (i) Slocs-v is the cortical indentation between the cSTS3 and lTOS. (ii) Slocs-d is the indentation between cSTS3/cSTS2 and IPS-PO. (iii) pAngs-v is the indentation between the cSTS2 and pips. (iv) pAngs-d is the indentation between cSTS2/cSTS1 and IPS. *(c)* The variability of the slocs and pAng components can cause them to disappear when individual surfaces are averaged together. Left to right: (i) 10 HCP participants, (ii) 20 HCP participants, (iii) 100 HCP participants, and iv) 650 HCP participants. The disappearance of these sulci on average surfaces, which are often used for group analyses in neuroimaging research, emphasizes the importance of defining these structures in individual hemispheres.

(ii) *Extracting and comparing the morphological and architectural features from sulcal labels*

Morphologically, we compared sulcal depth and surface area across sulci, as these are two of the primary morphological features used to define and characterize sulci [8,10–13,16–18,21,47–51]. As in our prior work [17,18], mean sulcal depth values (in standard FreeSurfer units) were computed in native space from the .sulc file generated in FreeSurfer [42] with custom Python code [17]. Briefly, depth values are calculated based on how far removed a vertex is from what is referred to as a "mid-surface," which is determined computationally so that the mean of the displacements around this "mid-surface" is zero. Thus, generally, gyri have negative values, while sulci have positive values. Each depth value was also normalized by the deepest point in the given hemisphere. Surface area (mm^2) was calculated with the FreeSurfer mris_anatomical_stats function (https://surfer.nmr.mgh.harvard.edu/fswiki/mris_anatomical_stats). The morphological features of all LPC/LPOJ sulci are documented in Supplemental figure 7.

Architecturally, we compared cortical thickness and myelination, as in our prior work in other cortical expanses [12,13,16,17]. Mean gray matter cortical thickness (mm) was extracted using the FreeSurfer mris_anatomical_stats function. To quantify myelin content, we used the T1-w/T2-w maps for each hemisphere, an in vivo myelination proxy [52]. To generate the T1-w/T2-w maps, two T1-w and T2-w structural MR scans from each participant were registered together and averaged as part of the HCP processing pipeline [44]. The averaging helps to reduce motion-related effects or blurring. Additionally, and as described by Glasser and colleagues [44], the T1-w/T2-w images were bias-corrected for distortion effects using field maps. We then extracted the average T1-w/T2-w ratio values across each vertex for each sulcus using custom Python code [12]. The architectural features of all LPC/LPOJ sulci are documented in Supplemental figure 7.

To assess whether these four metrics differed between the slocs-v and surrounding sulci (cSTS3 and lTOS), we ran a repeated measure analysis of variance (rm-ANOVA) with the within-participant effects of sulcus (slocs-v, cSTS3, and lTOS), metric (surface area, depth, cortical thickness, and myelination), and hemisphere (left and right). Rm-ANOVAs (including sphericity correction) were implemented with the aov_ez function from the afex R package. Effect sizes for the ANOVAs are reported with the partial eta-squared metric (η2). Post-hoc analyses were computed with the emmeans function from the emmeans R package (*p*-values corrected with Tukey's method). We also repeated these analyses for the three cSTS components [24,25] and the two intermediate parietal sulcal components (ips: aipsJ and pips [24,26]; detailed in the Supplemental Results and Supplemental Figure 8) as these components, to our knowledge, have not been quantitatively compared in previous work.

(f) <u>Functional analyses</u>

To determine if the slocs-v is functionally distinct from surrounding sulci, we generated functional connectivity profiles using recently developed analyses [12,13,53]. First, we used resting-state network parcellations for each individual participant from Kong and colleagues [54], who generated individual network definitions by applying a hierarchical Bayesian network algorithm to produce maps for each of the 17 networks in individual HCP participants. Importantly, this parcellation was conducted blind to both cortical folding and our sulcal definitions. Next, we resampled the network profiles for each participant onto the fsaverage cortical surface, and then to each native surface using CBIG tools (https://github.com/ThomasYeoLab/CBIG). We then calculated the spatial overlap between a sulcus and each of the 17 individual resting-state networks via the Dice coefficient (Equation 1):

$$(1) \quad \square\square\square\square(\square, \square) = \frac{2|\square \cap \square|}{|\square| + |\square|}$$

This process of calculating the overlap between each sulcus and the 17-network parcellation generated a "connectivity fingerprint" for each sulcus in each hemisphere of each participant. We then ran an rm-ANOVA with within-participant factors of sulcus (slocs-v, cSTS3, and ITOS), network (17 networks), and hemisphere (left and right) to determine if the network profiles (i.e., the Dice coefficient overlap with each network) of the slocs-v was differentiable from the surrounding sulci (i.e., cSTS3 and ITOS). Here we discuss effects related to networks that at least showed minor overlap with one sulcus (i.e., Dice ≥ .10). As in the prior analysis, we also repeated these analyses for the three cSTS components and the two intermediate parietal sulcal components (Supplemental Results and Supplemental Figure 8).

(g) <u>Behavioral analyses</u>

(i) *Model selection*

The analysis relating sulcal morphology to spatial orientation and/or reasoning consisted of using a cross-validated least absolute shrinkage and selection operator (LASSO) regression to select the sulci that explained the most variance in the data and determined how much variance is explained by sulcal depth as a predictor of behavior, as implemented in our previous work [16–18]. The depths of all LPC/LPOJ sulci were included as predictors in the LASSO regression model (Supplemental Methods for details on demographic control variables). As the shrinkage parameter (alpha) increases, it decreases the coefficient of each of the sulci to zero except for those with the strongest association. Therefore, this technique highlights the sulci whose morphology was most closely related to behavior. We used cross-validation to optimize the

shrinking parameter for the LASSO regression. Conventionally, we selected the model parameters that minimized the cross-validated mean squared error (MSE_{cv}) [55]. The optimization was performed with the GridSearchCV function sklearn in Python, which allowed us to determine the model parameters minimizing the MSE_{cv}. To evaluate the performance of any model selected by the LASSO regression, as in prior work [16–18], we measured the model performance for the relevant behavioral task using nested model comparison. With leave-one-out cross-validation (LooCV), we compared the LASSO-selected model with the predictors to a model with all left hemisphere sulci as predictors.

(ii) *Assessing morphological and behavioral specificity*

To assess whether our findings generalized to other anatomical features, we considered cortical thickness, which is consistently studied in cognitive neuroscience studies relating morphology to cognition [16–18,56,57]. To do so, we replaced sulcal depth with cortical thickness as the predictive metric in our LASSO-selected model. As with depth, the model was fit to the data with LooCV. To compare the thickness model to the depth model, we used the Akaike Information Criterion (AIC), which provides an estimate of in-sample prediction error and is suitable for non-nested model comparison. By comparing AIC scores, we are able to assess the relative performance of the two models. If the ΔAIC is > 2, it suggests an interpretable difference between models. If the ΔAIC is > 10, it suggests a strong difference between models, with the lower AIC value indicating the preferred model [58]. To also ascertain whether the relationship between LPC/LPOJ sulcal depth and cognition is specific to spatial orientation performance, or

transferable to other general measures of cognitive processing, we investigated the generalizability of the sulcal-behavior relationship to another widely used measure of cognitive functioning: processing speed [59]. Specifically, we used LooCV to predict processing speed instead of spatial orientation score. As with thickness, we compared the two models with the AIC.

Results

(a) Four previously undefined small and shallow sulci in the lateral parieto-occipital junction (LPOJ)

In addition to defining the 13 sulci previously described within the LPC/LPOJ, as well as the posterior superior temporal cortex (**Materials and Methods**) [24] in individual participants, we could also identify as many as four small and shallow sulci situated within the LPC/LPOJ that were more variable across individuals and uncharted until now (Supplemental Methods and Supplemental figures 1-4). Macroanatomically, we could identify two sulci between the cSTS3 and the IPS-PO/lTOS ventrally and two sulci between the cSTS2 and the pips/IPS dorsally.

Ventrally, we refer to these sulci as ventral (slocs-v; sulcus 5 in **figure 1**) and dorsal (slocs-d; sulcus 6 in **figure 1**) components of the supralateral occipital sulcus. The slocs-v, located between the posterior cSTS3 and lTOS, was present in 98.6% of hemispheres (left hemisphere: N = 71/72; right hemisphere: N = 71/72; **figure 1**). Conversely, the slocs-d, located between the cSTS3 and IPS-PO, was present 68.0% of the time (left hemisphere: N = 50/72; right hemisphere: N = 48/72; **figure 1**). Dorsally, we refer to the other newly identified sulci as the ventral (pAngs-v; sulcus 7 in **figure 1**) and dorsal (pAngs-d; sulcus 8 in **figure 1**) components of the posterior angular sulcus. The pAng components were more rare than the slocs components. Specifically, pAngs-v, located between cSTS2 and pips, was identifiable 31.3% of the time (19 left and 26 right hemispheres; **figure 1**). Located between cSTS2 and the

IPS, pAngs-d was identifiable only 13.2% of the time (8 left and 11 right hemispheres; **figure 1**). Though we characterize these sulci in this paper for the first time, the location of these four sulci is consistent with the presence of variable "accessory sulci" in this cortical expanse mentioned in prior modern and classic studies (Supplemental Methods).

These incidence rates were significantly different (GLM, main effect of sulcus: $\chi 2(3) = 166.53$, $p < .0001$; no hemispheric effects: *p*s > .68). The slocs-v was more common than the other three sulci (*p*s < .0001), slocs-d was more common than the pAngs components (*p*s < .0001), and pAngs-v was more common than pAngs-d ($p = .002$). We could further identify these sulci in post-mortem hemispheres (Supplemental figures 2, 3). Finally, to help guide future research on these newly- and previously-classified LPC/LPOJ sulci, we generated probabilistic maps of each of these 17 sulci and share them with the field with the publication of this paper (Supplemental figure 6; **Data accessibility statement**).

(b) <u>The slocs-v is morphologically, architecturally, and functionally dissociable from nearby sulci</u>

Given that the slocs-v was present in the majority of participants (98.6% across hemispheres), we focused our analyses on this stable sulcal feature of the LPOJ. To do so, we first tested whether the slocs-v was morphologically (depth and surface area) and architecturally (gray matter thickness and myelination) distinct from the two sulci surrounding it: the cSTS3 and lTOS (**figure 1**; Supplemental figure 7 for these metrics in all 17 sulci examined). An rm-ANOVA (within-participant factors: sulcus, metric, and hemisphere for standardized metric units) revealed a sulcus x metric interaction ($F(4, 276.19) = 179.15$, $\eta 2 = 0.38$, $p < .001$). Post hoc tests showed four main differences: (i) the slocs-v was shallower than cSTS3 ($p < .001$) but not lTOS ($p = .60$), (ii) the slocs-v was smaller than both the cSTS3 and lTOS (*p*s < .001), (iii) the slocs-v was thicker than both the cSTS3 and lTOS (*p*s < .001), and iv) the slocs-v was less

myelinated than both the cSTS and lTOS (*p*s < .001; **figure 2*a***). There was also a sulcus x metric x hemisphere interaction (F(4.20, 289.81) = 4.16, η2 = 0.01, *p* = .002; Supplemental Results).

We then tested whether the slocs-v was also functionally distinct from the cSTS3 and lTOS by leveraging resting-state network parcellations for each individual participant to quantify "connectivity fingerprints" for each sulcus in each hemisphere of each participant (**Materials and Methods**) [54]. An rm-ANOVA (within-participant factors: sulcus, network, and hemisphere for Dice coefficient overlap) revealed a sulcus x network interaction (F(32, 2144) = 80.18, η2 = 0.55, *p* < .001). Post hoc tests showed that this interaction was driven by four effects: (i) the cSTS3 overlapped more with the Default A subnetwork than both the slocs-v and lTOS (*p*s < .001), (ii) the slocs-v overlapped more with the Default C subnetwork than the lTOS (*p* < .001) and marginally than the cSTS3 (*p* = .077), (iii) the slocs-v overlapped more with the Dorsal Attention A subnetwork than both the cSTS3 and lTOS (*p*s < .001), and iv) the lTOS overlapped more with the Visual A and Visual B subnetworks than both the cSTS3 and slocs-v (*ps* < .004; **figure 2*b***). There was also a sulcus x network x hemisphere interaction (F(32, 2144) = 3.99, η2 = 0.06, *p* < .001; Supplemental Results). Together, these results indicate that the slocs-v is a morphologically, architecturally, and functionally distinct structure from its sulcal neighbors, and thus, deserves a distinct neuroanatomical definition.

We further found that the three caudal STS rami [24,25] and intermediate parietal sulci (aipsJ and pips) [24,26] are morphologically, architecturally, and functionally distinct structures for the first time (to our knowledge), which empirically supports their distinctions with separate sulcal labels (Supplemental Results and Supplemental figure 8).

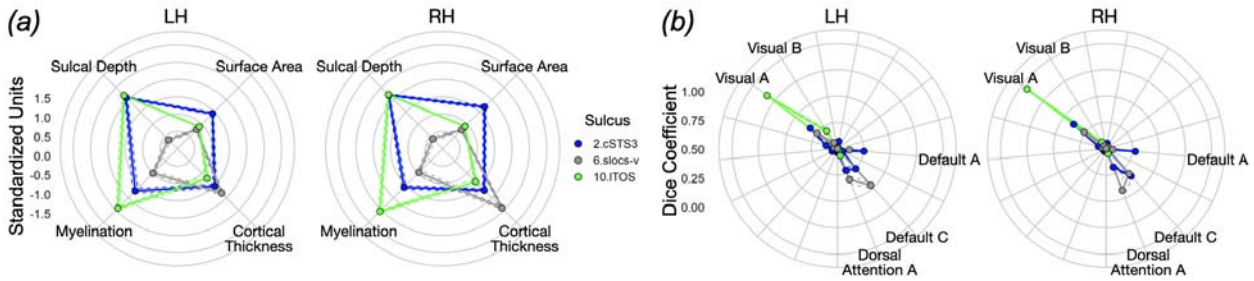

Figure 2. The slocs-v is morphologically, architecturally, and functionally dissociable from nearby sulci. *(a)* Radial plot displaying the morphological (upper metrics: depth, surface area) and architectural (lower metrics: cortical thickness, myelination) features of the slocs-v (gray), cSTS3 (blue), and lTOS (green). Each dot and solid line represent the mean. The dashed lines indicate ± standard error. These features are colored by sulcus (legend). Metrics are in standardized units. *(b)* Radial plot displaying the connectivity fingerprints of these three sulci: the Dice Coefficient overlap (values from 0-1) between each component and individual-level functional connectivity parcellations [54].

(c) <u>The morphology of LPC/LPOJ sulci, including the slocs-v, is related to cognitive performance</u>

Finally, leveraging a data-driven approach of cross-validated LASSO feature selection, we sought to determine whether sulcal depth, a main defining feature of sulci, related to cognitive performance (**Materials and Methods**). To do so, we primarily focused on spatial orientation and reasoning given that these abilities recruit multiple subregions of lateral parietal and/or occipital cortices [38–41]. As in prior work [16–18], we chose the model at the alpha that minimized MSE_{cv}. Participants with a slocs-v in both hemispheres and all behavioral metrics were included (N = 69). Due to their rarity (being in less than 70% of hemispheres at most), we did not include the slocs-d or pAng components in this analysis.

This method revealed an association between spatial orientation scores and normalized sulcal depth in the left hemisphere (MSE_{cv} = 25.63, alpha = 0.05; **figure 3*a***), but not in the right hemisphere (MSE_{cv} = 26.41, alpha = 0.3). Further, we found that no LPC/LPOJ sulci were selected for reasoning in either hemisphere (right*:* alpha = 0.3, MSE = 24.01; left: alpha = 0.3, MSE = 24.01). Six left hemisphere LPC/LPOJ sulci were related to spatial orientation task

performance **figure 3a, *b***). Four of these sulci were positioned ventrally: cSTS3 (β = -9.77), slocs-v (β = -3.36), lTOS (β = -4.91), and mTOS (β = -0.06), whereas two were positioned dorsally: pips (β = 5.02), and SPS (β = 4.30; **figure 3a, *b***). Using LooCV to construct models that predict behavior, the LASSO-selected model explained variation in spatial orientation score (R^2_{cv} = 0.06, MSE_{cv} = 23.99) above and beyond a model with all left hemisphere sulci (R^2_{cv} < 0.01, MSE_{cv} = 27.12). This model also showed a moderate correspondence (r_s = 0.29, p = .01; **figure 3*c***) between predicted and actual measured scores. We then tested for anatomical and behavioral specificity using the AIC, which revealed two primary findings. First, we found that the LASSO-selected sulcal depth model outperformed a model using the cortical thickness of the six LASSO-selected sulci (R^2_{cv} < .01, MSE_{cv} = 26.02, $AIC_{cortical\ thickness} – AIC_{sulcal\ depth}$ = 2.19). This model also showed task specificity as these sulci outperformed a model with processing speed (R^2_{cv} < .01, MSE_{cv} = 254.65, $AIC_{processing\ speed} – AIC_{spatial\ orientation}$ = 63.57). Thus, our data-driven model explains a significant amount of variance on a spatial orientation task and shows behavioral and morphological specificity.

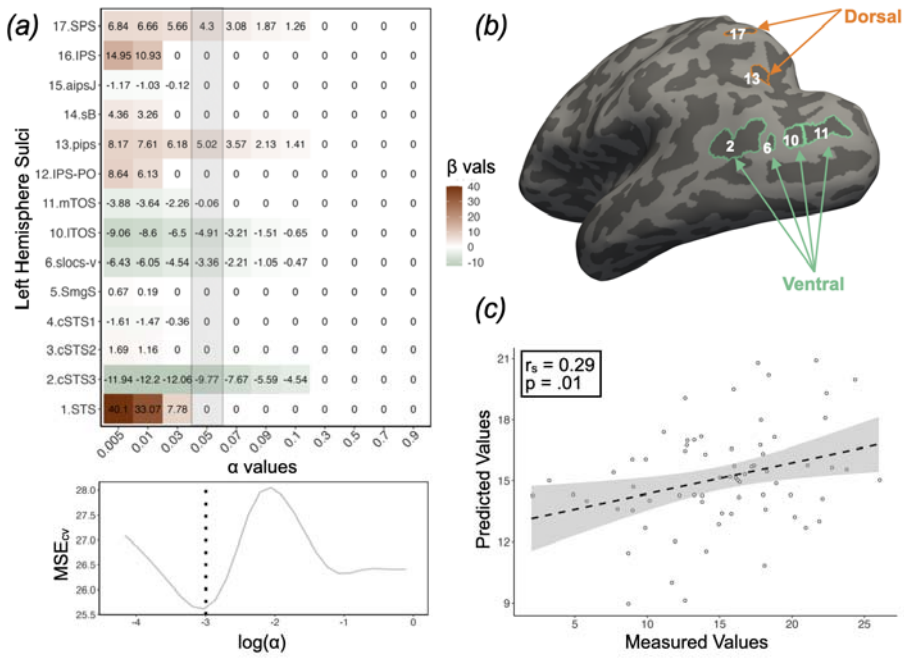

Figure 3. The morphology of LPC/LPOJ sulci, including the slocs-v, is related to cognitive performance. *(a)* Beta-coefficients for each left hemisphere LPC/LPOJ sulcus at a range of shrinking parameter values [alpha (α)]. Highlighted gray bar indicates coefficients at the chosen α-level. Bottom: Cross-validated mean-squared error

(MSE_{CV}) at each α level. By convention, we selected the α that minimized the MSE_{CV} (dotted line). *(b)* Inflated left hemisphere cortical surface from an example participant highlighting the two groups of sulci—*dorsal positive* (orange) and *ventral negative* (green)—related to spatial orientation performance. *(c)* Spearman's correlation (r_s) between the measured and the predicted spatial orientation scores from the LASSO-selected model is shown in *(a)*.

Discussion

(a) Overview

In the present study, we examined the relationship between LPC/LPOJ sulcal morphology, functional connectivity fingerprints, and cognition. We report five main findings. First, while manually defining sulci in LPC/LPOJ across 144 hemispheres, we uncovered four new small and shallow sulci that are not included in present or classic neuroanatomy atlases or neuroimaging software packages. Second, we found that the most common of these structures (the slocs-v; identifiable 98.6% of the time) was morphologically, architecturally, and functionally differentiable from nearby sulci. Third, using a model-based, data-driven approach quantifying the relationship between sulcal morphology and cognition, we found a relationship between the depths of six LPC/LPOJ sulci and performance on a spatial orientation processing task. Fourth, the model identified distinct dorsal and ventral sulcal networks in LPC/LPOJ: ventral sulci had negative weights while dorsal sulci had positive weights (**figure 3*b***). These findings are consistent with previous neuroimaging work from Gur et al. [41] who demonstrated separate functional activations in dorsal parietal and the more ventrally situated occipital-parietal cortices for the judgment of line orientation task used in the present study. Fifth, the model identified that the slocs-v is cognitively relevant, further indicating the importance of this new neuroanatomical structure. In the sections below, we discuss (i) the slocs-v relative to modern functional and cytoarchitectonic parcellations in the LPC/LPOJ, as well as anatomical connectivity to other parts of the brain, (ii) underlying anatomical mechanisms relating sulcal morphology and

behavior more broadly, and (iii) limitations of the present study. Implications for future studies are distributed throughout each section.

(b) <u>The slocs-v relative to modern functional and cytoarchitectonic parcellations in the LPC/LPOJ, as well as anatomical connectivity to other parts of the brain</u>

To lay the foundation for future studies relating the newly-identified slocs-v to different anatomical and functional organizational features of LPC/LPOJ, we situate probabilistic predictions of slocs-v relative to probabilistic cortical areas identified using multiple modalities. For example, when examining the correspondence between the slocs-v and modern multimodal (HCP-MMP [37]) and observer-independent cytoarchitectural (Julich-Brain atlas [60]) areas (Supplemental Methods), the slocs-v is located within distinct areas. In particular, the slocs-v aligns with the multimodally- and cytoarchitecturally-defined area PGp bilaterally and cytoarchitecturally-defined hIP4 in the right hemisphere (**figure 4**). In classic neuroanatomical terms [61], this indicates that the slocs-v is a putative “axial sulcus” for these regions, which future work can assess with analyses in individual participants.

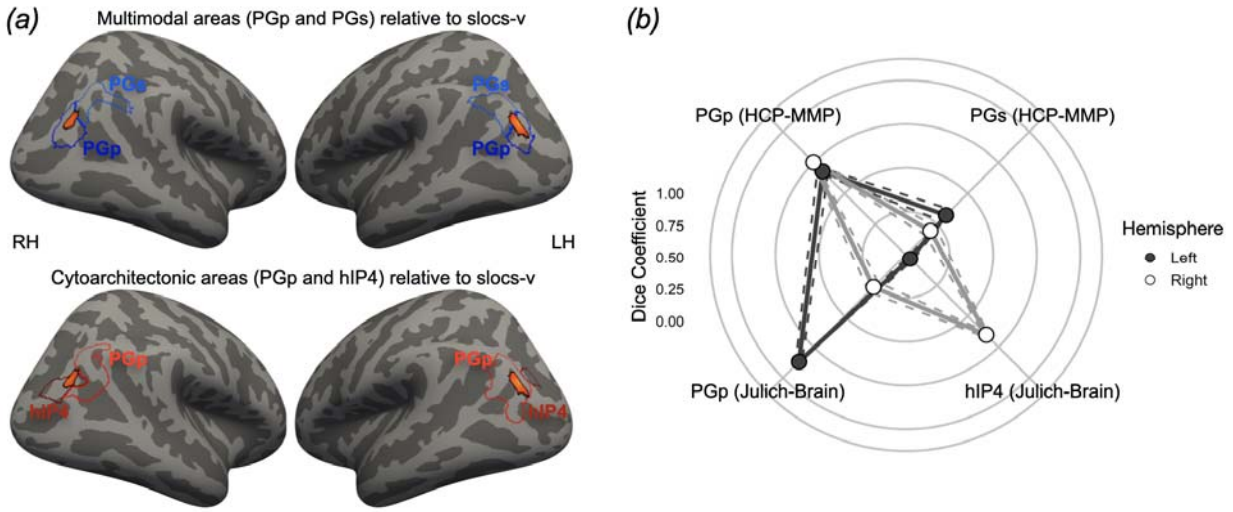

Figure 4. The slocs-v relative to modern functional and cytoarchitectonic parcellations in LPC/LPOJ. *(a)* Top: Left (LH) and right (RH) hemispheres of the inflated fsaverage surface with two areas from the modern HCP multimodal parcellation (HCP-MMP; blue) [37] relative to an MPM of the slocs-v (warm colors indicate areas with at least 20% overlap across participants; Supplemental figure 6). Bottom: Same as top, except for two observer-independent cytoarchitectonic regions from the Julich-Brain Atlas [60]. *(b)* Overlap between the slocs-v and each area (Supplemental Methods). Each dot and solid line represents the mean. The dashed lines indicate ± standard error (left: gray; right: white).

Aside from recent multimodal and observer-independent cytoarchitectonic parcellations, an immediate question is: What is the relationship between the slocs-v and other functional regions at this junction between the occipital and parietal lobes, as well as potential anatomical connectivity? For example, there are over a dozen visual field maps in the cortical expanse spanning the TOS, IPS-PO, and the IPS proper (see (i), (ii), and (iii), respectively in **figure 5*a***) [33]. When projecting probabilistic locations of retinotopic maps from over 50 individuals from Wang and colleagues [62] (Supplemental Methods), the slocs-v is likely located outside of visual field maps extending into this cortical expanse (**figure 5*a***). Nevertheless, when also projecting the map of the mean R^2 metric from the HCP retinotopy dataset from 181 participants shared by Benson and colleagues [63] (Supplemental Methods), the slocs-v is in a cortical expanse that explains a significant amount of variance (left hemisphere: R^2_{mean} = 19.29, R^2_{max} = 41.73; right hemisphere: R^2_{mean} = 21.17, R^2_{max} = 44.23; **figure 5*b***).

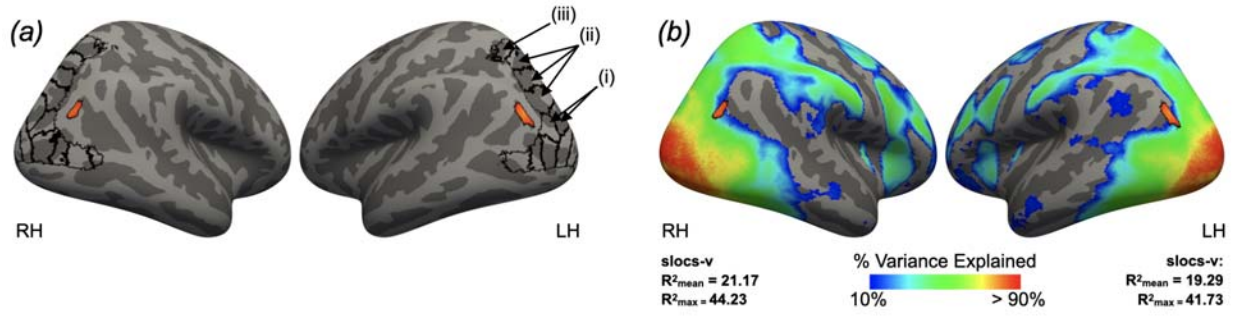

Figure 5. The slocs-v relative to retinotopy. *(a)* Top: Left (LH) and right (RH) hemispheres of the inflated fsaverage surface displaying the probabilistic locations of retinotopic maps from over 50 individuals from Wang and colleagues [62] (black outlines). The predicted slocs-v location from the MPMs is overlaid in orange (as in figure 4). (i), (ii), and (iii) point out the retinotopic maps in the cortical expanse spanning the TOS, IPS-PO, and IPS, respectively. *(b)* Same format as in *(a)*, but with a map of the mean R^2 metric from the HCP retinotopy dataset [63] overlayed on the fsaverage surfaces (thresholded between R^2 values of 10% and 90%). This metric measures how well the fMRI time series at each vertex is explained by a population receptive field (pRF) model. The mean and max R^2 values for the slocs-v MPM in each hemisphere are included below each surface.

In terms of anatomical connectivity, as the slocs-v co-localizes with cytoarchitectonically defined PGp (**figure 4**) and previous studies have examined the anatomical connectivity of the probabilistically defined PGp, we can glean insight regarding the anatomical connectivity of slocs-v from these previous studies [64,65]. This prior work showed that PGp was anatomically connected to temporooccipital regions, other regions in the temporal lobe, middle and superior frontal cortex, as well as the inferior frontal cortex and insula [64,65]. Of course, the location of the slocs-v relative to multimodal, cytoarchitectonic, and retinotopic areas, as well as the anatomical connectivity of the slocs-v, would need to be examined in individual participants, but the present work makes clear predictions for future studies as fleshed out here. To conclude this section, as the multimodal area PGp (**figure 4**) was recently proposed as a "transitional area" by Glasser and colleagues [37] (Supplemental table 1), future studies can also further functionally and anatomically test the transitional properties of slocs-v.

(c) <u>Underlying anatomical mechanisms relating sulcal morphology and behavior</u>

In this section, we discuss potential anatomical mechanisms contributing to the relationship between sulcal depth and behavior in two main ways. First, long-range white matter fibers have a gyral bias, while short-range white matter fibers have a sulcal bias in which some fibers project directly from the deepest points of a sulcus [66–70]. As such, recent work hypothesized a close link between sulcal depth and short-range white matter properties [16–18,71,72]: deeper

sulci would reflect even shorter short-range white matter fibers, which would result in faster communication between local, cortical regions and in turn, contribute to improved cognitive performance. This increased neural efficiency could underlie individual differences in cognitive performance. Ongoing work is testing this hypothesis which can be further explored in future studies incorporating anatomical, functional, and behavioral measures, as well as computational modeling.

Second, our model-based approach identified separate dorsal and ventral sulcal networks in which deeper sulci dorsally and shallower sulci ventrally contributed to the most explained variance on the spatial orientation task. A similar finding was identified by our previous work in the lateral prefrontal cortex [18]. These previous and present findings may be explained by the classic anatomical compensation theory, which proposes that the size and depth of a sulcus counterbalance those of the neighboring sulci [23,48,73]. Thus, a larger, deeper sulcus would be surrounded by sulci that are smaller and shallower, rendering the overall degree of cortical folding within a given region approximately equal [23,48,73]. Future work can incorporate underlying white matter architecture into the compensation theory, as well as a recent modification that proposed to also incorporate local morphological features such as the deepest sulcal point (e.g., sulcal pit or sulcal root [74]), which has recently been shown to be related to different functional features of the cerebral cortex [50,51,75]. Altogether, these and recent findings begin to build a multimodal mechanistic neuroanatomical understanding underlying the complex relationship between sulcal depth and cognition relative to other anatomical features.

(d) Limitations

The main limitation of our study is that presently, the most accurate methodology to define sulci —especially the small, shallow, and variable tertiary sulci—requires researchers to manually

trace each structure on the cortical surface reconstructions. This method is arduous and time-consuming, which, on the one hand, limits the sample size in terms of number of participants, while on the other, results in thousands of precisely defined sulci - a push-pull relationship reflecting a conversation in the broader human brain mapping and cognitive neuroscience fields between a balance of large N studies and “precision imaging” studies in individual participants [76–79]. Though our sample size is comparable to other studies that produced reliable results relating sulcal morphology to brain function and cognition (e.g., [3,4,8,10,12,13,17–19,46]), ongoing work that uses deep learning algorithms to automatically define sulci should result in much larger sample sizes in future studies [80,81]. Finally, the time-consuming manual definitions of primary, secondary, and tertiary sulci also limit the cortical expanse explored in each study, thus, restricting the present study to LPC/LPOJ.

(e) <u>Conclusion</u>

In conclusion, we uncovered four previously-undefined sulci in LPC/LPOJ and quantitatively showed that the slocs-v is a stable sulcal landmark that is morphologically, architecturally, and functionally differentiable from surrounding sulci. We further used a data-driven, model-based approach relating sulcal morphology to behavior, which identified different relationships of ventral and dorsal LPC/LPOJ sulcal networks contributing to the perception of spatial orientation. The model identified the slocs-v, further indicating the importance of this new neuroanatomical structure. Altogether, this work provides a scaffolding for future “precision imaging” studies interested in understanding how anatomical and functional features of LPC/LPOJ relate to cognitive performance at the individual level.

Ethics statement

Human participants: HCP consortium data were previously acquired using protocols approved by the Washington University Institutional Review Board (Mapping the Human Connectome: Structure, Function, and Heritability; IRB # 201204036). Informed consent was obtained from all participants. The data are treated according to the WU-Minn HCP Consortium data use terms and the terms of use for the restricted data.

Competing interests statement

The authors declare no competing financial interests.

Data accessibility statement

The processed and anonymized HCP neuroimaging data required to perform all statistical analyses and reproduce all figures used for this project are available on GitHub (https://github.com/cnl-berkeley/stable_projects/tree/main/Updating_LPOJ_sulci) and Dryad (DOI: doi:10.5061/dryad.rbnzs7hh9) repositories. The analysis pipelines are available on Open Science Framework (https://osf.io/7fwqk/).

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